THE PELECANIFORM CHARACTERS OF THE SKELETON OF THE SHOE-BILL STORK, *BALAENICEPS REX*

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THE PELECANIFORM CHARACTERS OF THE SKELETON OF THE SHOE-BILL STORK, *BALAENICEPS REX*

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INTRODUCTION

In the course of rearranging the bird skeletons in the collections of the British Museum (Natural History) it seemed to me that the skeleton of *Balaeniceps rex* had more pelecaniform than ciconiiform characters. The position of *Balaeniceps* in orthodox classifications is, and nearly always has been, near the storks and herons, so that this anomalous impression of its affinities seemed to require detailed investigation. The results of this study are presented here. The skeletal characters of *Balaeniceps rex* have been reassessed in relation to stork-like and heron-like characters on the one hand, and pelican-like characters on the other.

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HISTORICAL NOTE

There are few important original contributions to the knowledge of *Balaeniceps's* affinities. Gould, who described the bird in 1850, called it the " Grallatorial type of the Pelecanidae ", although he also noted that its external features resembled " in general contour " those of *Grus*, *Ardea* and *Cochlearius*. Jardine (1851) noted likenesses to herons in the plumage. He considered that differences from the " true " pelicans, in the nostrils, pouch, position of the laryngeal opening and the absence of webs on the feet, were sufficient to show that *Balaeniceps* was not closely related

to them. Von Heuglin (1856 : 60) placed it between *Anastomus* and *Dromas* in his systematic list. Bonaparte (1855 : 143) put it in the same subfamily as *Cochlearius*, describing it as intermediate between the pelicans and the Boat-bill. Des Murs (1859 : 480) considered that the egg was like that of *Phoenicopterus*.

These were the conflicting opinions in 1860 when Parker examined the skeleton of *Balaeniceps*. He was impressed by its similarities to *Scopus* and *Cochlearius*, especially the latter, and indicated many characters which it had in common with the " Ardeine " birds. Although the storks were included in his term " Ardeine ", he seemed to stress the heron-like characters of *Balaeniceps* because he considered it to be a large edition of *Cochlearius*. He noted some similarities to the Pelecaniformes but attributed them to convergence. Bartlett's discovery (1861) of powder-down on *Balaeniceps* seemed to add weight to Parker's conclusions. Reinhardt (1860), unaware of Parker's work, found more similarities with *Scopus* than *Cochlearius* in the external characters of *Balaeniceps*, and considered that *Balaeniceps* and *Scopus* were nearer the storks than the herons. In 1861, after reading an abstract of Parker's paper, he compared a skull of *Balaeniceps* with those of *Scopus* and *Cochlearius*, but still maintained that *Balaeniceps* was related to *Scopus* and the storks. The similarities between the skulls of *Balaeniceps* and *Cochlearius* he attributed to convergence. Parker admitted (1862) that he knew nothing of the anatomy of *Scopus* when he wrote his paper, but, having seen a live *Balaeniceps*, he remained convinced of its likeness to the herons. He regarded *Ardea* as the " central type " of the storks and herons, linked to *Cochlearius* and *Scopus* by *Balaeniceps*.

These two opinions became established. Some authors agreed with Reinhardt's conclusions and placed *Balaeniceps* with *Scopus* and the storks, but most of them agreed with Parker and placed it with *Cochlearius* and the herons. Giebel (1873) showed that the pectination of the middle claw and the pterylosis of *Balaeniceps* are similar to those of *Scopus* and different from *Cochlearius*. Beddard (1888) compared the visceral anatomy with that of the storks, herons and *Scopus* and, because of the alimentary tract, powder-down patches and syrinx, concluded that *Balaeniceps* was allied to the herons. Like Beddard, Furbringer (1888) and Gadow (1893 : 137) agreed with Parker. So did Shufeldt (1901), who wrote a paper on the osteology of *Scopus* and *Balaeniceps* without having seen a skeleton of the latter.

The next important contribution was made by Chalmers Mitchell (1913) who dissected a specimen and described many more anatomical details. It is interesting that he could find no outstanding characters which indicated affinities with the herons rather than the storks, or vice-versa. He noted that *Scopus* and *Balaeniceps* had many similarities, and that they had characters common to both herons and storks. When he took each character at its face value he found *Balaeniceps* had more in common with the storks than the herons, so he decided to put it in the same suborder as *Scopus*, storks and ibises. He acknowledged that this was an arbitrary rather than a phylogenetic arrangement. He noted several similarities to the pelicans, but thought they occurred because the pelicans were related to the storks and herons.

Böhm (1930) studied the structure of the skulls of juvenile and adult *Balaeniceps*. After a comprehensive investigation he concluded that Reinhardt's, Parker's, Giebel's and his own researches showed *Balaeniceps* to be a typical stork, linking the storks to the herons. He mentioned the " outstanding relationship " between *Balaeniceps* and *Pelecanus*, but did not seem to think it significant because he thought *Pelecanus* itself was so different from the other Pelecaniformes. The only other investigations of *Balaeniceps's* anatomy were made by Technau (1937 : 567) during his studies of the nasal cavity of birds, and by Glenny (1955 : 560) in his work on the aortic arches of birds. The former drew no conclusions as to *Balaeniceps's* affinities, though Glenny thought it less like the Ciconiidae than is usually supposed.

After Chalmers Mitchell's contribution most authors placed *Balaeniceps* by itself in a group of equal rank with the herons and storks (e.g. Streseman, 1927–34 : 809 ; Wetmore, 1930 : 3). Mayr & Amadon (1951 : 6), however, followed Böhm's suggestion and placed it with the typical storks in the family Ciconiidae. Wetmore's classification (1951 revision) shows the generally accepted taxonomic position of *Balaeniceps* in relation to the orders Pelecaniformes and Ciconiiformes.

Order Pelecaniformes.
- Suborder Phaëthontes.
  - Family Phaëthontidae.
- Suborder Pelecani.
  - Superfamily Pelecanoidea.
    - Family Pelecanidae.
  - Superfamily Suloidea.
    - Family Sulidae.
      - Phalacrocoracidae.
      - Anhingidae.
- Suborder Fregatae.
  - Family Fregatidae.

Order Ciconiiformes.
- Suborder Ardeae.
  - Family Ardeidae.
    - Cochlearidae.
- Suborder Balaenicipites.
  - Family Balaenicipitidae.
- Suborder Ciconiae.
  - Superfamily Scopoidea.
    - Family Scopidae.
  - Superfamily Ciconioidea.
    - Family Ciconiidae.
  - Superfamily Threskiornithoidea.
    - Family Threskiornithidae.
- Suborder Phoenicopteri.
  - Family Phoenicopteridae.

METHODS

As the purpose of this study is to examine the pelecaniform characters of *Balaeniceps's* skeleton in relation to its ciconiiform characters, the composition of the Pelecaniformes and Ciconiiformes will be discussed to decide what *Balaeniceps* ought to be compared with.

The living members of the Pelecaniformes are apparently not very alike. Nearly every genus is placed in a separate family. From a comparison of their osteology it seems that the differences are mainly due to adaptive radiation, and that there is a well-defined basic similarity. For instance, superficially, pelicans and cormorants look less alike than storks and herons, but their skeletons have more characters in common. A possible exception is *Phaëthon*, which is peculiar in many respects and may not be closely related to the rest of the Pelecaniformes. Wetmore (1951 : 5) thinks that " the Phaëthontes possibly may have separated earlier than the Fregatae " from the pelecaniform stock. Therefore, as *Phaëthon* is atypical the Phaëthontes will not be referred to in this investigation. The Fregatae are also considered aberrant by some authors, but they have so many of the osteological characters typical of the Pelecani that they are probably fairly closely related to them.

The Ciconiiformes is basically a less uniform group than the Pelecaniformes. Osteologically, it seems to be a collection of unrelated groups which, superficially, only have long beaks, long necks and long legs in common.

The genera of the Ardeae are very alike, their outstanding variation being in size. *Cochlearius* is the most aberrant genus but, apart from its skull, it has all the characters of the typical herons. Even in its skull the heron-like characters are not completely obscured. For the present purpose, therefore, the Ardeidae and Cochlearidae will be considered together, as a monophyletic group representing the herons.

The families in the Ciconiae are not so closely related. The Scopidae, with its single monotypic genus *Scopus*, is as enigmatic in its relationships as *Balaeniceps*. The skeleton of *Scopus* is like that of a small stork in some characters, but very unlike it in others. It has often been compared with *Balaeniceps*, and most authors consider the two related. However, there is no point in comparing one genus of doubtful affinities with another, so *Scopus* will not be referred to. The Ciconiidae is probably a monophyletic group ; its genera are fairly alike, although they vary more than those of the Ardeidae. This variation mainly seems to be due to different adaptations of the beak, correlated with differences in the size and shape of the head. The third family, Threskiornithidae, appears to have much in common with the Ciconiidae, but it also has certain resemblances to the Phoenicopteri. As the affinities of the Phoenicopteri themselves are controversial it is advisable not to discuss either group until their relationships have been more fully investigated.

For the purposes of this investigation, therefore, *Balaeniceps* is compared with the suborders Pelecani and Fregatae, representing the Pelecaniformes ; the ciconiiform suborder Ardeae, representing the typical herons ; and the family Ciconiidae, representing the typical storks.

Three complete skeletons of *Balaeniceps* and three skulls were available. There was also adequate material of pelicans and their allies, frigate birds, herons and storks. The skeleton of *Balaeniceps* was systematically compared with those of *Pelecanus, Ardea* amd *Ciconia,* but other genera, especially in the Pelecaniformes, were consulted to determine the range of variation in each group.

For convenience, in the following description *Nannopterum, Halietor* and *Anhinga* will not be mentioned unless they differ from *Phalacrocorax.*

OSTEOLOGICAL CHARACTERS

A. *Skull,* see Plate 3

(1) *Premaxilla*

Of the Pelecaniformes considered here, *Pelecanus, Phalacrocorax* and *Fregata* each have a well developed hook at the tip of the premaxilla. The newly hatched chick of *Sula* also has this hook, but it decreases with age, and in the adult the tip of the premaxilla is only slightly decurved. *Anhinga* has no hook in chick or adult, but this may be an adaptation to its habit of spearing fish.

In the Ciconiidae there is no suggestion of a hook to the premaxilla in any of the genera. The nearest approach is the decurved bill of *Ibis* and *Mycteria,* but in these the distal fifth of the mandible is involved in the curvature.

The Ardeidae have straight bills. Parker (1862 : 299) argues that in *Cochlearius* a hook " certainly does exist, although feebly " but, although the tip of the rhamphotheca is decurved, it is not hooked, and the premaxilla is quite straight ventrally.

Balaeniceps has a prominent hook at the tip of the premaxilla, like the typical Pelecaniformes.

(2) *Nasal groove*

In the Pelecani and Fregatae there is a conspicuous groove running along each side of the culmen from the anterior edge of the nostril to the cutting edge of the premaxilla beside the terminal hook. This relationship of the nasal groves to the premaxillary hook is constant in *Pelecanus, Sula, Phalacrocorax* and *Fregata.* In *Anhinga* the groves are only faintly indicated.

In the Ciconiidae the nasal groves are either absent, or represented by very shallow depressions which extend from the nostrils to, at most, half-way along the beak. Both conditions are often found in the same species.

The Ardeidae have shallow depressions like those of the Ciconiidae instead of nasal grooves. In *Cochlearius* these depressions are expanded to form broad, shallow troughs, each with a ridge along the mesial border.

Balaeniceps has conspicuous nasal groves which extend from the nostril to the cutting edge of the premaxilla beside the terminal hook, exactly as they do in the Pelecani and Fregatae. The grooves are not shallow, like those of the Ardeidae and Ciconiidae, or broad like those of *Cochlearius,* but deep like those of *Pelecanus.*

(3) *Nasal septum*

In the Pelecani and Fregatae there is an ossified nasal septum. The nasal septum of the Ciconiidae and Ardeidae is not ossified, and it is perforated in the region of the external nares. *Cochlearius* has a complete, unossified nasal septum. In *Balaeniceps* the nasal septum is ossified, as it is in the Pelecani and Fregatae.

(4) *Nasal passage*

In *Pelecanus* the external nares are vertically above, or even slightly posterior to the internal nares, and the nasal cavity lies almost vertically between them. In the other Pelecani the external nares are only slightly anterior to the internal nares. In the Ciconiidae and Ardeae the external nares are an appreciable distance anterior to the internal nares, and the nasal cavity lies obliquely between them. In *Balaeniceps* the relative positions of the nares and nasal cavity are exactly the same as they are in *Pelecanus*.

(5) *Palate* (See Fig. 1)

In the Pelecani and Fregatae the palatines are always ankylosed along the mid-line posterior to the internal nares. There is usually a median ventral ridge, more or less well developed, along the suture, with a depression for the pterygoid muscle on either side of it. These depressions extend forwards past the posterior edge of the internal narial opening only in *Fregata*. In the region of the internal nares the mesial edges of the palatines are parallel in the Pelecani, and nearly so in the Fregatae. In *Pelecanus* the ventral part of the nasal passage is divided along the mid-line by a membranous septum. There is no trace of an ossified prevomer in association with this septum, and in *Sula* the septum itself is weakly developed. The septum is better developed in *Phalacrocorax*, and in at least one species, *P. urile*, there is a thorn-like cartilaginous prevomer associated with it (unless it is carefully dissected out the prevomer is easily lost in prepared skeletons of *Phalacrocorax*). In *Fregata* the prevomer is also thorn-like, though longer and definitely ossified. The maxillopalatines vary in size throughout the Pelecani and Fregatae. In *Sula* and *Phalacrocorax* they are small and do not project beyond the palatines mesially. They are slightly larger in *Fregata*, and can be seen, in ventral view, bordering the anterior half of the internal nasal opening. In *Pelecanus* they are very large and meet in the mid-ventral line between the anterior ends of the palatines. Also in *Pelecanus*, they nearly fill the inside of the skull in the nasal region, and their posterior edges slant backwards in a straight line from the internal nares to the cranio-facial hinge. Posteriorly, the maxillopalatines do not extend past the cranio-facial hinge-line in any of the Pelecani or Fregatae.

The palatines of the Ciconiidae are not fused along the mid-line except at one point. Instead of the median ventral ridge found in the pelicans, there is a ventral crest along the mesial edge of each palatine where it borders the internal narial opening. The depressions for the pterygoid muscles extend further forward on either side of the narial opening than in *Fregata*. Immediately anterior to the internal nares the

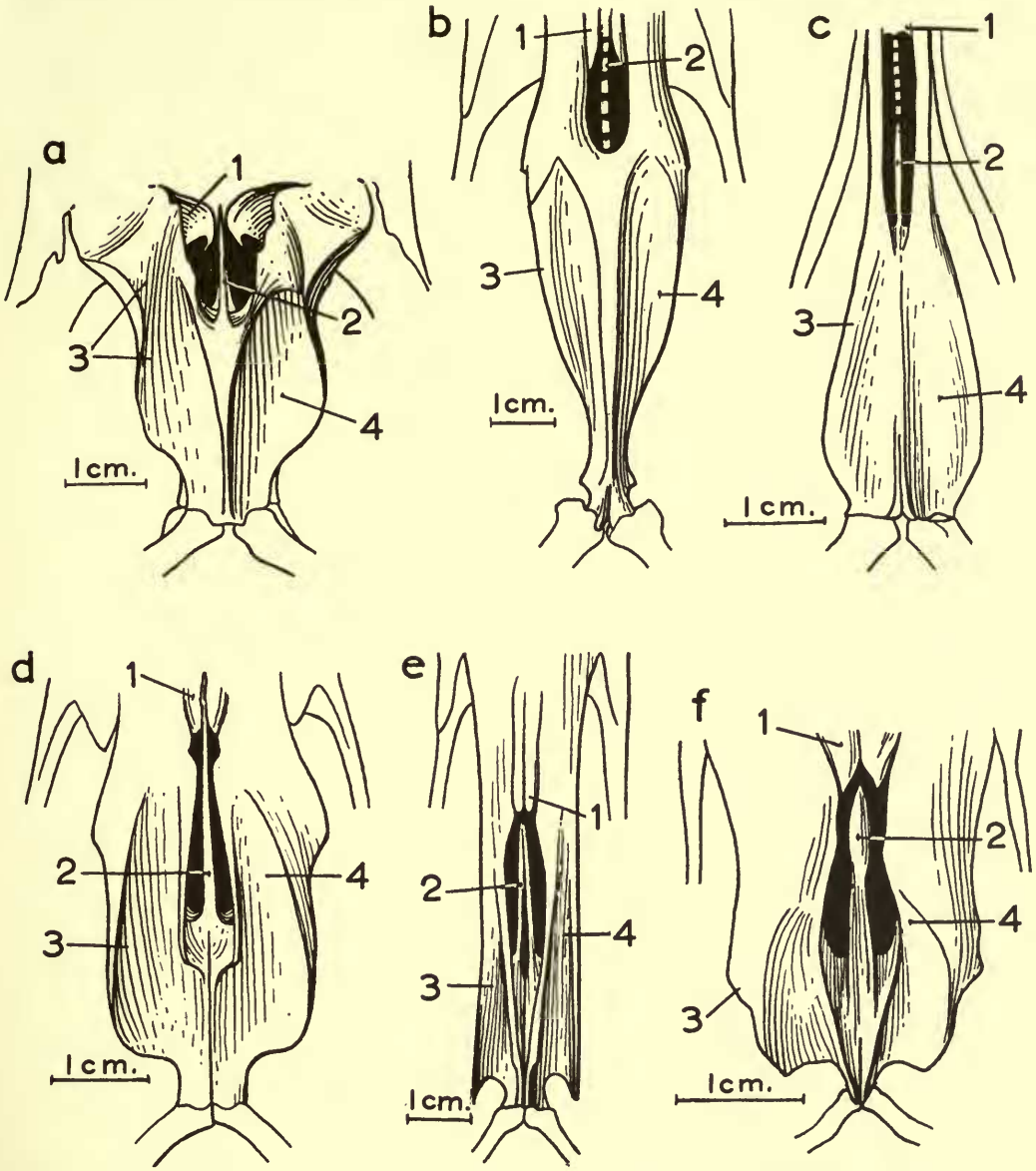

FIG. 1. Diagrams of ventral views of palatine regions of (a) *Balaeniceps rex*, (b) *Pelecanus crispus*, (c) *Phalacrocorax urile*, (d) *Ciconia ciconia*, (e) *Ardea goliath*, (f) *Cochlearius cochlearius*.

1 = maxillopalatine, 2 = prevomer, or position of unossified septum, 3 = palatine, 4 = depression for pterygoid muscle.

palatines approach the mid-line, and in the larger genera, such as *Leptoptilos* and *Jabiru*, they may even touch. This divides the space between them into anterior and posterior parts, the nasal passage being confined to the posterior part. The prevomer arises at the posterior end of the internal narial opening, and the palatines are ankylosed at this point. The prevomer varies from a narrow strip of bone in *Ibis*, to a substantial triangular plate, drawn out into a thin filament anteriorly, in *Leptoptilos* and the larger genera. The maxillopalatines are well developed when compared with those of most Pelecani and Fregatae. They always meet in the mid-ventral line, where they occupy most of the space between the palatines anterior to the internal nares. Each maxillopalatine is extended posteriorly into a convex projection which usually reaches beyond the cranio-facial hinge; in the Pelecani there is no such projection.

The palatines of the Ardeidae are like those of the Ciconiidae except that they are separate along the mid-line, even where the prevomer arises. In *Cochlearius*, however, they are ankylosed at this point, as they are in the Ciconiidae. The depressions for the pterygoid muscles extend as far forwards on either side of the internal narial opening as they do in the Ciconiidae. In the Ardeae, unlike the two previous groups, the vomer is V-shaped in cross-section, though this is less obvious in *Cochlearius*. The maxillopalatines meet in the mid-ventral line anterior to the nasal opening, much as they do in the Ciconiidae. Their posterior edges are convex like those of the Ciconiidae, and extend well beyond the level of the cranio-facial hinge. The maxillopalatines are smaller in *Cochlearius*, but otherwise they are very like those of the Ardeidae.

In *Balaeniceps* the palatines are ankylosed along the mid-line, posterior to the internal nares, with a broad ventral ridge along the suture. The depressions for the pterygoid muscles lie on either side of this ridge; they extend forward to the level of the nasal aperture, but no further. The condition of the palatines is thus very like that of *Pelecanus*. The prevomer is weakly developed and its degree of ossification varies in the specimens examined. It is a thin, triangular plate, often perforated, lying in a vertical plane. In some specimens the apex does not reach the anterior end of the nasal opening. This weak development of the prevomer is reminiscent of the Pelecani, in which the prevomer is reduced and sometimes missing. The maxillopalatines are strikingly like those of *Pelecanus*. Their posterior faces are flat, even concave, and not convex like those of the Ciconiidae and Ardeae (Pycraft, 1898 : 83).

(6) *Lachrymal* (See Fig. 2)

The lachrymal in the Pelecani and Fregatae descends from the frontal to the quadratojugal bar, to which it is usually attached by a ligament. Viewed posteriorly, it is a column of bone with a lateral groove, of varying depth, to accommodate the lachrymal duct. In *Phalacrocorax* a narrow lateral process of the interorbital septum meets and fuses with the ventral end of the lachyrymal. This process is larger in *Anhinga*, lying beside the lachrymal throughout its length without touching it. In lateral view, the lachrymal is more or less pillar-shaped in *Pelecanus*,

Fregata and *Phalacrocorax*, but in *Sula* it is expanded anteriorly into the antorbital vacuity. There is a tendency, in the Pelecani and Fregatae, for this vacuity to be reduced. In *Pelecanus* it is comparatively large. In *Fregata* the maxilla grows back into it a little posteriorly. In *Phalacrocorax* there is a splint of bone resting on the quadratojugal bar. This bone fills most of the antorbital vacuity in *Anhinga*, in which the maxilla is produced posteriorly as well. The large lachrymal itself fills most of the antorbital vacuity in *Sula*, though the maxilla and the quadratojugal also expand into it.

Although the lachrymal is well developed in the larger Ciconiidae, it never reaches the quadratojugal bar. In posterior view it is roughly triangular, with the apex of the triangle downwards. In some genera, including the four largest, the lachrymal

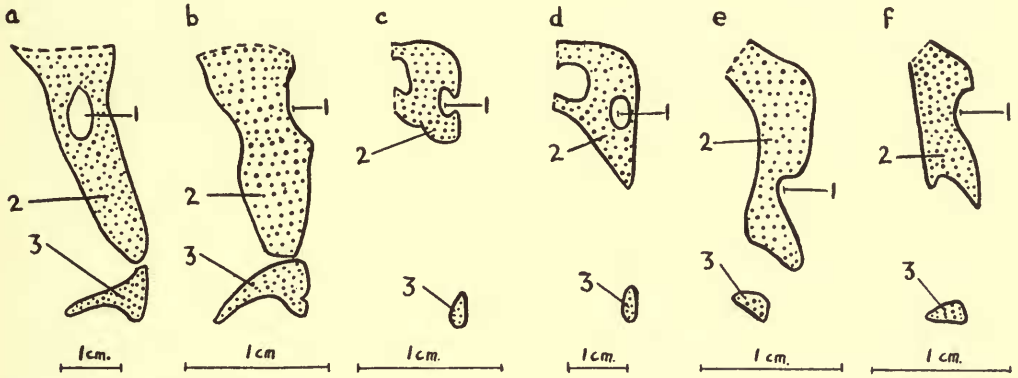

FIG. 2. Diagrammatic transverse sections of lachrymals of (a) *Balaeniceps*, (b) *Sula*, (c) *Ciconia*, (d) *Leptoptilos*, (e) *Ardea*, (f) *Cochlearius*.
1 = lachrymal duct, 2 = lachrymal bone, 3 = quadratojugal bar.

duct is wholly or partly enclosed in bone, giving a flat surface to the outer face of the lachrymal bone. Unlike the Pelecani or Fregatae, the ciconiid lachrymal has a mesial projection extending towards the interorbital septum and passing ventral to the duct of the nasal gland. The lachrymal is triangular in cross-section, and it never extends into the antorbital vacuity. This vacuity is large in the Ciconiidae, and there is no obvious tendency for the surrounding bones to expand into it.

In the Ardeidae the lachrymal nearly reaches the quadratojugal bar. Its shape seems to be peculiar to the Ardeidae and is quite different from the Pelecani, Fregati and Ciconiidae. In *Cochlearius* the lachrymal is reduced, and in lateral view looks different from that of the Ardeidae ; but in cross-section it is almost identical. The antorbital vacuity is large in the Ardeidae and in *Cochlearius*.

Balaeniceps has a large lachrymal. In posterior view it is like the lachrymal of the Pelecani and Fregatae, a column of bone which meets the quadratojugal bar ventrally. The lacrymal duct lies in a large foramen through the lachrymal bone, as it does in some Ciconiidae. Anteriorly, the lachrymal fuses with the maxilla, so that the antorbital vacuity is obliterated. There is a slight groove which may

represent the suture between the lachrymal and the maxilla. If it does, the lachrymal is pillar-shaped in lateral view as it is in the Pelecani and Fregatae. The complete occlusion of the antorbital vacuity, which occurs in *Balaeniceps*, is not found in any of the other groups considered here, but the Pelecani and Fregatae have a tendency towards reduction of the size of the antorbital vacuity.

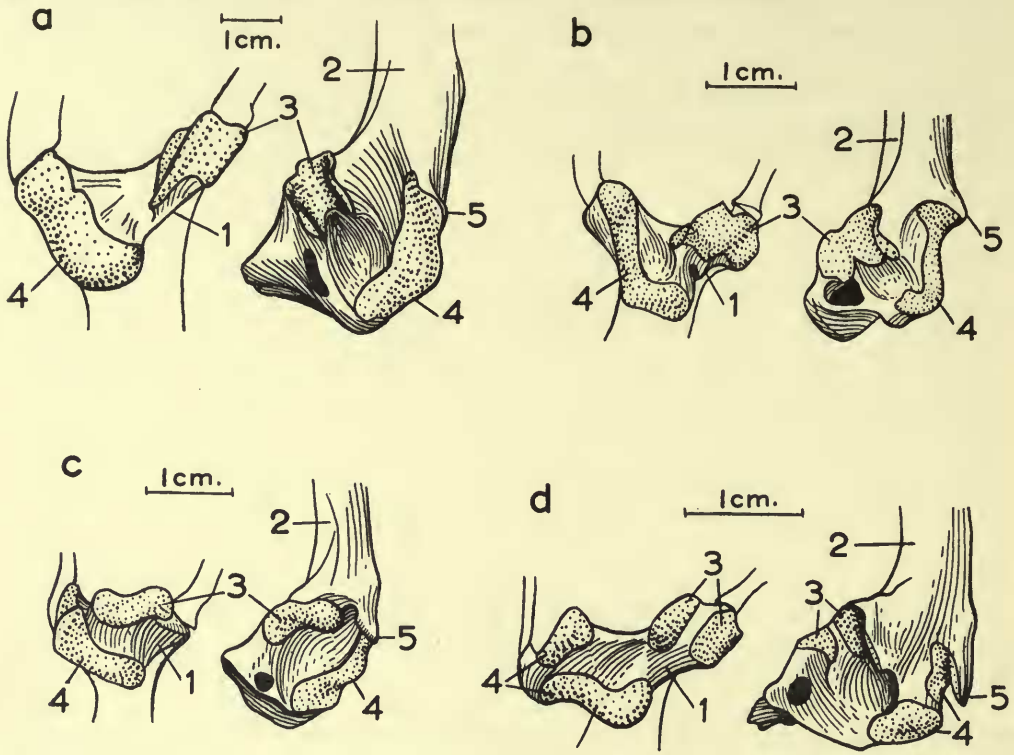

FIG. 3. Diagrams of articulating surfaces of quadrates and lower jaws of (a) *Balaeniceps rex*, (b) *Sula bassanus*, (c) *Ciconia ciconia*, (d) *Cochlearius cochlearius*.
1 = left quadrate, 2 = left ramus of lower jaw, 3 = mesial articulating facets, 4 = lateral articulating facets, 5 = lateral process.

(7) *Lower jaw articulation* (See Fig. 3)

Each of the three groups being compared with *Balaeniceps* has a different arrangement of the articulating surfaces of the quadrate and lower jaw. The arrangement is constant within each group, except that the one typical of the Ardeidae is found mainly in the larger species.

In the Pelecani and Fregatae there are two articulating facets. On the quadrate, the mesial articulation has a broad ridge, which slides in a corresponding trough in the lower jaw. The long axis of the articulation lies at an angle of about 45° to the long axis of the skull, and is in line with the long axis of the pterygoid. This is

especially noticeable in *Pelecanus*. In *Sula, Fregata* and *Phalacrocorax* the lateral edge of this ridge on the quadrate is undercut, and the corresponding side of the groove in the lower jaw is overhanging. The result is a locking mechanism which, in the dried skull, is efficient enough to hold the lower jaw in place when the beak is closed. The lateral articulation is usually S-shaped, though in *Sula* it may be L-shaped. Its long axis lies approximately at right angles to that of the other articulation. In *Pelecanus*, possibly because of its wide gape, the lateral part of this articulation is modified. In the lower jaw, instead of a sigmoid articular surface there is a groove, running anteriorly, parallel to the mid-line. Along this groove slides part of the lateral articulating surface of the quadrate. This groove in the lower jaw is represented in *Sula* by a shallow transverse trough, the anterior side of which projects laterally and dorsally and lies anterior to the lateral process of the quadrate when the beak is closed. The lateral process on the lower jaw is reduced in *Fregata* and *Phalacrocorax*.

The Ciconiidae also have two articulating facets. Unlike the Pelecani and Fregatae the long axis of the mesial facet is at right angles to the long axis of the skull, and at an angle of about 120° to the pterygoid. There is no locking mechanism. The lateral articulation is curved, so that while its lateral end is at right angles to the long axis of the mesial articulation, its mesial end is parallel to it. The lateral process on the lower jaw is well developed. The relationship between the two facets is quite different from that found in the pelicans or herons, and it is very alike in all the Ciconiidae examined, whatever the relative proportions of bill and skull.

In most of the larger Ardeidae there are four articulating facets, as each of those occurring in the pelicans and storks is in two parts. The lateral part of the mesial facet and the mesial part of the lateral facet lie on a plane nearly parallel to the pterygoid. On the quadrate the mesial facet, although it is in two parts, is undercut laterally to give a locking mechanism, as it is in most of the Pelecani and Fregatae. The lateral process on the lower jaw is more prominent than in the other groups described. In *Cochlearius* the articulating facets are essentially the same as in the larger herons, but the mesial facet on the quadrate is undercut mesially as well as laterally, apparently increasing the efficiency of the locking mechanism. The lateral process on the lower jaw is even better developed than in the Ardeidae, and, with the lateral part of the lateral articulation, seems to function as an auxillary locking device.

Balaeniceps has two undivided articular facets, like the Pelecani, Fregate and Ciconiidae. On the quadrate, the mesial facet consists of a broad ridge, undercut laterally, which, in the lower jaw, slides in a trough with an overhanging lateral edge, much as it does in *Sula, Phalacrocorax* and *Fregata*. The mesial side of the trough also overhangs slightly, but not as much as in *Cochlearius*. The axis of the mesial articulation on the quadrate is in line with the pterygoid, as it is in the Pelecani and Fregatae, and is in contrast to the condition in the Ciconiidae. The lateral articulation is L-shaped, as it is in *Sula* ; its long axis is nearly at right angles to that of the mesial facet, like the Pelecani and Fregatae, and unlike the Ciconiidae. In the lower jaw, the lateral process is insignificant and the lateral articulation takes no

part in the locking mechanism as it does in *Cochlearius*. *Balaeniceps* has none of the well defined ciconiid characters in its jaw articulation ; it resembles the Ardeae in some ways, but differs in others ; it is like the Pelecani and Fregatae in all the characters in which they differ from the Ciconiidae and Ardeae.

B. *Pectoral Girdle* (See Fig. 4)

(1) *Furculum*

There is a tendency in the Pelecani and Fregatae for the hypocleideum of the furculum to be fused to the keel of the sternum. The joint is ligamentous in *Phalacrocorax* ; sometimes ankylozed in *Sula* ; usually ankylosed in adults of *Pelecanus* ; and so ossified in adults of *Fregata* that the suture is obliterated. Except in *Fregata* each arm of the furculum forms an arc, convex anteriorly, between each coracoid and the carina sterni. Characteristic of the typical pelecaniform pectoral girdle is the well developed acrocoracoid flange, which forms a flat transverse surface on the clavicle for articulating with the coracoid. In *Fregata* the clavicle is completely fused to the coracoid in this region, but in young specimens the presence of the acrocoracoid flange can be inferred from the sutures. Although an acrocoracoid flange is present in several other apparently unrelated groups, it is never as well developed as it is in the Pelecani, Fregatae, *Balaeniceps* and *Scopus*.

In the Ciconiidae, although the hypocleideum of the furculum joins the carina sterni, it forms a bony fusion with it only in some specimens of one genus, *Leptoptilos*, and the suture is always obvious. Unlike the Pelecani, each clavicle forms a sigmoid curve in lateral view. The dorsal part of the curve is convex anteriorly, and the ventral part, where the clavicles unite in the mid-line is concave anteriorly. There is no indication of an acrocoracoid flange in any of the Ciconiidae.

The furculum of the larger Ardeae is mainly like that of the Ciconiidae. The joint between the hypocleideum and the carina sterni is always ligamentous. The presence of a small interclavicle is characteristic of the Ardeae, and it is not found in the other groups considered here.

The hypocleideum of *Balaeniceps* is fused to the carina sterni as it is in *Fregata* and most adult specimens of *Pelecanus*. The suture is obliterated by ossification in all the British Museum specimens. The clavicle of *Balaeniceps* forms a continuous arc from the coracoid to the carina sterni, as it does in the Pelecani. This character may not be significant, as the clavicle of *Fregata* is in a slightly sigmoid curve and that of *Cochlearius* is almost in a continuous curve. The acrocoracoid flange is well developed in *Balaeniceps*, a character typical of the Pelecaniformes.

(2) *Sternum*

In *Balaeniceps* the sternal keel extends along the whole length of the sternum to the posterior border as it does in the Ciconiidae, Ardeae and most other birds. In *Pelecanus*, *Sula* and *Phalacrocorax* it only reaches half-way back from the anterior end of the sternum. Parker (1860 : 329) considered this a significant difference between *Balaeniceps* and the Pelecani, but apparently was not aware of the condition

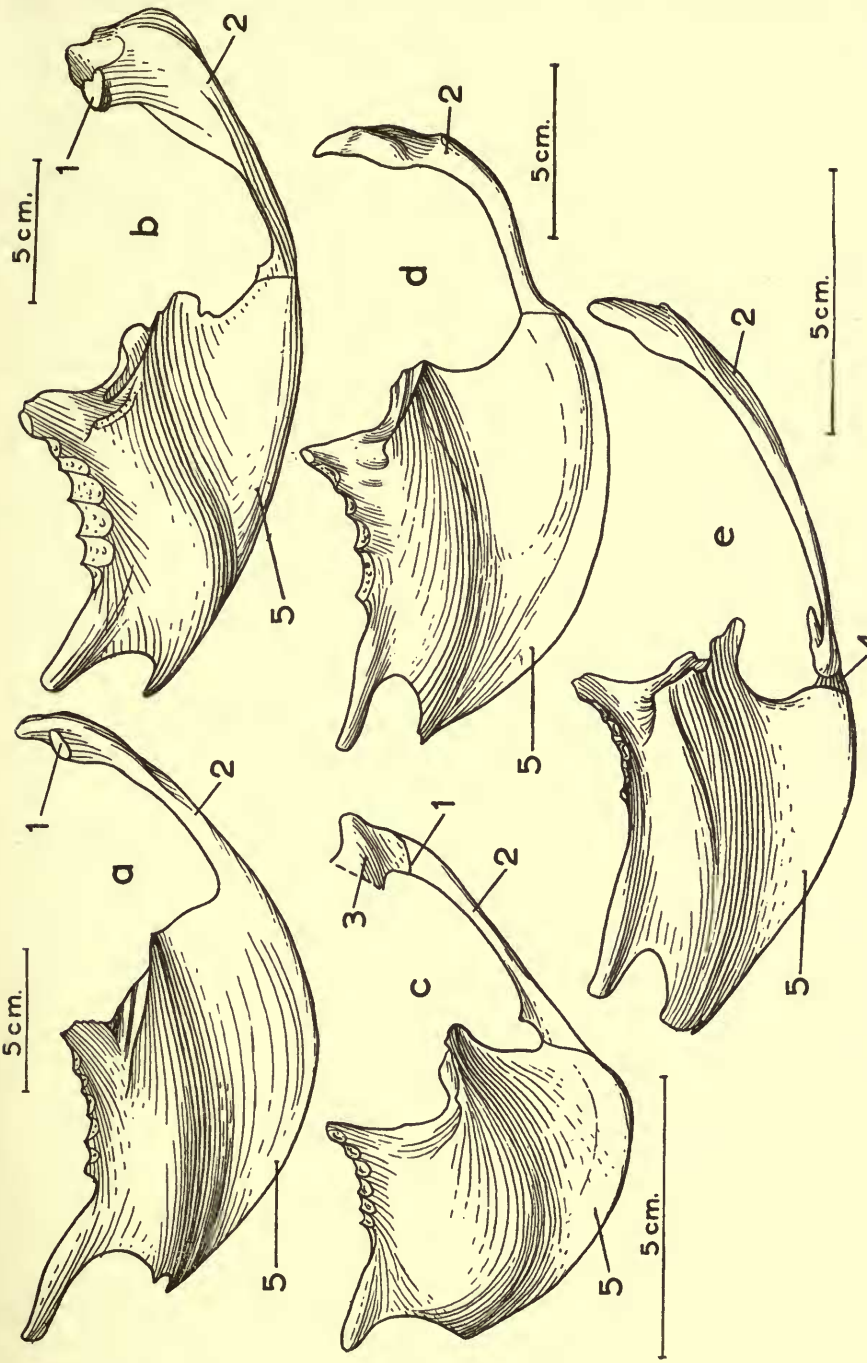

FIG. 4. Diagrams of lateral views of sterna of (a) *Balaeniceps rex*, (b) *Pelecanus erythrorhynchuse*, (c) *Fregata ariel*, (d) *Ciconia ciconia*, (e) *Ardea goliath*.
1 = Acrocoracoid flange, 2 = clavicle, 3 = coracoid,
4 = ligament, 5 = sternum.

in *Fregata*, in which the keel extends almost to the posterior end of the sternum. Thus within the Pelecaniformes both types of keel occur.

c. *Pelvic Girdle*

Parker (1861 : 336) considered the pelvis of *Balaeniceps* to be " typically ardeine " because it was narrow like that of the Ardeae. Chalmers Mitchell (1913 : 696) thought it more like the ciconiid pelvis because it had a notch in the posterior border, like the Ciconiidae, and lacked the ridge on the ilium which is present in the Ardeae. However, the shape and details of the pelvis in birds seem to depend mainly on the function and relative size of the legs and leg muscles, and the pelvis is probably a very adaptable part of the skeleton. In the Pelecaniformes, for example, the pelvis of *Pelecanus*, a bird with strong legs, seems to have very little in common with that of *Phalacrocorax*, in which the legs are weaker and used mainly for swimming, or of *Fregata*, in which the legs are very weak and only used for perching. In groups in which there is less adaptive radiation, such as the Ciconiidae, or Ardeae, the function of the legs is more uniform and the shape of the pelvis varies little within the group, the main differences being in size. In *Balaeniceps* the pelvis is roughly the same shape as it is in the Ardeae and some Ciconiidae, but it differs from both in details. It seems even less like that of any of the Pelecaniformes, but as there is already a good deal of variation of the pelvis in this group *Balaeniceps* would perhaps be less out of place with them than with the Ciconiidae or Ardeae.

d. *Hind Limb*

(1) *Tibio-tarsus*

There are two forms of the distal condyles and the inter-condylar sulcus of the tibio-tarsus in the groups considered here. One is found in the Pelecani, Fregatae and Ardeae. In it the distal condyles are roughly semicircular in lateral view and the distal border of the outer condyle has no notch. The anterior aspect of the inter-condylar sulcus is fairly shallow, and the knob on the tarso-metatarsus which fits into it is not well developed. This type of articular surface is probably unspecialized, as it occurs throughout the Pelecani and Fregatae, in which there is considerable variation in the function of the legs, and in the Ardeae, in which the legs are long and unlike those of any of the pelican groups.

A second form occurs in the Ciconiidae. In it the distal borders of the condyles are flattened, and the condyles themselves are elongated posteriorly, so that they are oval in lateral view. There is a notch in the distal border of the outer condyle. The anterior aspect of the inter-condylar sulcus is deep, and proximal to it there is a hemispherical depression with a prominent knob immediately beside it. The knob on the tarso-metatarsus is much larger than in the first type, and articulates with the hemispherical depression when the leg is bent. The second condition apparently only occurs in long-legged birds, such as the Threskiornithidae and Phoenicopteridae, and to a lesser extent in the Gruidae and long-legged Charadrii.

The form in *Balaeniceps* is similar to that of the Pelecani, Fregatae and Ardeae.

(2) *Tarso-metatarsus*

In most groups of birds the hypotarsus is well ossified to form a varying number of " bridges " which enclose the flexor tendons in bony tubes. Of the Pelecani, *Phalacrocorax* has one tube and *Sula* and *Pelecanus* two.

In contrast, the Ciconiidae have a so-called " simple " hypotarsus. It consists of two parallel bony ridges with a groove between. The flexor tendons lie in this groove and are supported by unossified ligaments instead of bony bridges.

The Ardeae have a more ossified hypotarsus, rather like that of the Pelecani. In most genera there is only one tube, but the smaller genera sometimes have more.

Balaeniceps has two complete bony tubes through the hypotarsus. Their arrangement is strikingly like that of *Pelecanus*, and quite unlike the Ciconiidae.

(3) *First metatarsal*

In the Ciconiidae and Ardeae the first toe points backwards. In the Pelecani it is joined to the second toe by a web and is restricted to a lateral position, although it is mobile enough to be able to be pointed forwards. Parker (1861 : 344) says that in *Balaeniceps* the first toe is " very mobile " and is turned " very far inwards " when walking. Photographs show that it is directed backwards when the bird is standing still.

The position of the first toe influences the form of the first metatarsal. When the toe normally points backwards the metatarsal, if straight, would lie in the same plane as the flexor tendons of the other digits and interfere with their functioning. But the shape of the metatarsal is modified, usually giving it the appearance of bending round to one side of the tendons, and it often has a diagonal groove in which the tendons run freely.

In *Pelecanus*, in which the first toe does not point backwards, the metatarsal is straight, with only a shallow depression, mid-way along its length, where it touches the flexor tendons. In the other Pelecani this depression varies in size and depth, but it is never so marked as it is in the Ciconiidae and Ardeae. In *Sula* and *Phalacrocorax* the metatarsal is slightly bent round the flexor tendons.

In the Ciconiidae there is a broad, deep, diagonal trough for the flexor tendons, and the metatarsal appears twisted through an angle of about 90°. In the Ardeae the first metatarsal does not press against the flexor tendons as closely as it does in the Ciconiidae, because of the way in which it articulates with the first phalanx. As a result the diagonal groove in which the tendons lie is less marked than it is in the Ciconiidae and narrower than it is in the Pelecani.

In *Balaeniceps* the metatarsal has a depression for the flexor tendons which is very little deeper than that of *Pelecanus*. It is shallower than that of the Ciconiidae and broader than that of the Ardeae. The metatarsal appears slightly twisted, though less so than it is in the Ciconiidae. The form of the first metatarsal and the function of the first toe of *Balaeniceps* therefore seem to be more like those of the Pelecani than the Ciconiidae or Ardeae.

(4) *Toe articulations*

The proximal articulating surfaces of the basal phalanges of the second, third and fourth digits are fairly alike in the Pelecani and Ciconiidae, being roughly square in shape. In the Ardeae each of these articulating surfaces has a characteristic, irregular shape. *Balaeniceps* is like the first two groups, with the articulations almost square in proximal view.

SOME NON-SKELETAL PELECANIFORM CHARACTERS OF *BALAENICEPS*

(*a*) von Heuglin (1873 : 1095)

The egg is white with chalky lumps. Similar chalky lumps and nodules occur on eggs of *Phalacrocorax* and *Sula*.

Birds join up in parties to herd shoals of fish into corners. This communal fishing is characteristic of some *Phalacrocorax* and *Pelecanus* species.

(*b*) Chalmers Mitchell (1913)

The rhamphotheca is compound, as it is in the Pelecani and Fregatae.

A pyloric chamber is present in the stomach, as in *Pelecanus*.

The dermo-temporalis, biventer maxillae, temporal and pterygoid muscles are similar in *Pelecanus*.

There are no intrinsic muscles of the syrinx in *Balaeniceps* and *Pelecanus*.

The hyoid muscles are " excessively like those of *Pelecanus*."

The division of the pectoral muscle is similar in *Pelecanus*.

The arrangement of the wing tendons is the same in *Pelecanus*.

(*c*) Technau (1936 : 567)

The secondary nostrils can be closed, as in *Pelecanus*.

(*d*) Glenny (1955)

The right carotid is absent in *Balaeniceps* and some Pelecaniformes. When one carotid is missing in the Ciconiiformes it is the left one.

DISCUSSION

Those who have studied *Balaeniceps's* affinities from its skeleton seem to have been mainly concerned with its heron-like or stork-like features, and have neglected to consider its likeness to the pelicans. Jardine (1852) may have been responsible for this when he noted what he thought were significant differences from the " true pelicans ". Earlier impressions of *Balaeniceps* however were that it was near the pelicans. For example, its first mention in literature was by Ferdinand Werne (1848 : 143) who recorded that on 15th December 1840, " During my siesta someone saw a water bird that seemed to be as big as a young camel, which actually had a beak just like a pelican's, only without the pouch beneath it ". Even Gould (1852) referred to it as a kind of pelican, and Chalmers Mitchell (1913 : 701) considered that this opinion was " at least as happy as the more confident statements of later writers". None of the non-pelican characters given by Jardine are skeletal. No

evidence from comparative osteology has been given as a reason for not putting *Balaeniceps* with the Pelecaniformes, although this has usually been implied on the few occasions when differences between *Balaeniceps* and the Pelecaniformes have been described. For example, Parker (1860 : 329) when describing the sternum, mentions that the keel extends to the posterior end of the sternum in *Balaeniceps*, as it does in the storks and herons, " whereas in the Pelicans, Gannets and Cormorants it scarcely continues beyond the middle of that bone ".

On the other hand, skeletal characters common to *Balaeniceps* and the Pelecaniformes have often been referred to. Sometimes they have been attributed to convergence (Parker 1861 : 308), or to the " common inheritance " of the Pelecaniformes and Ciconiiformes (Chalmers Mitchell 1913 : 699), but more often they are mentioned without comment or even without reference to the fact that they occur in both *Balaeniceps* and the Pelecaniformes. These characters are summarized below. They are arranged under three headings, and when a character is mentioned by more than one author, or under more than one heading, it is only referred to the first time it occurs on the list. Only original works are referred to. An asterisk is placed against the characters considered in the present investigation.

CHARACTERS OF BALAENICEPS'S *SKELETON THAT ALSO OCCUR IN THE PELECANIFORMES.*

A. *Noted and commented on by authors*

Parker (1861 : 308)

* The palatines have the " same essential structure " in other fish eating birds, such as the Pelican, Cormorant and Gannet, because the " motions of the upper jaw on the cranium " are the same.

Chalmers Mitchell (1913 : 699)

* Long lachrymals.
* Mesial ankylosis of the palatines.
Shell-like paroccipital processes.
* Clavicle ankylosed to carina sterni.
Shape of the head of the humerus.

He says these are either due to " convergent modifications between birds which, after all, are not very far apart in the system " or to the " common inheritance " of the Pelecaniformes and " their immediate allies ".

Böhm (1930 : 700)

Balaeniceps resembles *Pelecanus* in its closed palate.
* Hook to premaxilla.
* Bony nasal septum.
Complete interorbital septum.
Well developed postorbital process.
Lack of a postangular process on the lower jaw.

He says the Pelecaniformes are more like the herons than the storks, except for *Pelecanus* which is atypical, and more like the storks and *Balaeniceps*.

B. *Noted by authors, without comment*

Parker (1860)

Cervical vertebrae have haemal arches (p. 328).
* Furculum articulates with acrocoracoid flange (p. 329).
Tongue is small (p. 330).

Parker (1861)

" General class resemblance " in occipital region (p. 275).
Sudden bend in furculum (p. 340).

Chalmers Mitchell (1913)

* Nasal groove (p. 690).

C. *Mentioned by authors, without reference to the Pelecaniformes*

Parker (1861)

* Arrangement of the articulating surfaces of the quadrate and lower jaw (p. 310).
Ischium is longer than ilium posteriorly (p. 337).
No prepubic process (p. 337).
Wing skeleton—Parker says this is like that of the herons (p. 342) ; I found it as much like that of *Pelecanus* as *Ardea*.
Well developed " cnemial ridges " in tibio-tarsus (p. 343).
Slight sigmoid curve at distal end of tibio-tarsus (p. 343).
" Anterior cavity " at proximal end of tarso-metatarsus is deeper than in *Ardea* (p. 343).
* Complex hypotarsus (p. 344).
* Mobile hallux (p. 344).

Chalmers Mitchell (1913)

A rounded notch separates the metasternum from the posterior lateral processes of the sternum (p. 694).
Bases of coracoids do not meet in the mid-line (p. 696).
A notch separates the posterior ends of the ilium and ischium (p. 696).
No horizontal ridge formed by the " dorso-lateral edge of the post-acetabular ilium " (p. 696).
A tibial bridge is present (p. 697).

Of these skeletal characters common to *Balaeniceps* and the Pelecaniformes, some have been described as being due to " convergence " and others to " common inheritance ". It is one of the problems of taxonomy to distinguish between these two causes. In this instance the problem is to determine what are significant taxonomic characters in the pelecaniform skeleton. At the same time it might not

be out of place to refer to the wider problem of the taxonomic significance of osteological characters One point of view is that bone is not an easily adapted substance, and that therefore phylogeny is readily determined from an examination of the skeleton. Verheyen (1953 : 480), for example, says that " systematics based on comparative osteology is perfectly realizable " since osteological characters are " practically invariable " and are " sheltered from the adaptations and modifications imposed by frequent habit ". There is clearly a good deal of truth in this, but it is a point of view that should be regarded with caution. There is evidence to show that bone is a plastic substance readily moulded by any change in the forces exerted by the muscles attached to it. This opinion is expressed, for example, by Weinmann & Sicher (1947 : 120) who say, " if it be true that functional stresses shape the bone, then it is equally true that a change of strength or direction of forces will lead to changes in the form and structure of bones ". Changes in muscle function related to changes in habit are therefore reflected in the skeleton. Similarities in habit of unrelated species and differences in habit of related species can produce a crop of adaptive osteological characters which may obscure phylogeny. Phylogeny may be apparent only in a number of small characters which have been relatively unaffected by adaptive changes. The sum of these characters may be peculiar to a particular group. Although the members of such a group vary in appearance and habit, and show convergence with other groups, they will have most of the small characters typical of their group. These " non-adaptive " characters differ from group to group and may occur in different parts of the skeleton, so that each group must be studied separately to get the " feel " of its typical characters.

In the light of these observations it will be understood that a " pelicaniform character " is hard to define precisely. The skeletal characters considered here are mainly those which distinguish the Pelecani and Fregatae from the Ciconiidae and Ardeae. Some of them, for example the acrocoracoid flange, also occur in other groups of birds. For this reason authors have not regarded it as important that *Balaeniceps* has them (Chalmers Mitchell, 1913 : 695). However, they have been included here because it is now understood that any given character may be taxonomically significant in one group, but not necessarily in another (e.g. see Cain, 1954 : 268). The acrocoracoid flange distinguishes the Pelecani, Fregatae and *Balaeniceps* from the Ciconiidae and Ardeae, but not from the Scopidae, Falconiformes, most Charadriiformes, Columbidae, Strigiformes, some Procellariiformes, and many other groups. It is not intended to imply that all the groups with an acrocoracoid flange are related, or that any of them are necessarily more closely related to the pelicans than to the storks.

Not all the " pelicaniform characters " considered here occur throughout the Pelecani and Fregatae. Sometimes one genus, or more, may differ in one feature from the others. For example, adults of *Anhinga* and *Sula* have no hook at the tip of the premaxilla, but they are typical in most other respects.

In other cases there may be a general trend, or tendency within the group, towards a certain condition, though all the genera are not necessarily concerned in it. One example of this is the tendency for reduction of the antorbital vacuity. In

Pelecanus, the antorbital vacuity is large, as it is in most birds ; in *Fregata*, *Phalacrocorax*, *Anhinga* and *Sula* it becomes progressively reduced. *Balaeniceps*, therefore, with no antorbital vacuity, would complete the series.

Sometimes an underlying pattern can be traced in a structure, with differences in details in each genus. A good example of this is the arrangement of the quadrate condyles in the jaw articulation (see Text-figures). The general form of the nasal cavity and of the palate possibly come into this category. In each of these instances *Balaeniceps* has the same underlying pattern as the Pelecaniformes, but the storks and herons do not.

To sum up, the general skeletal features which can be described as " pelecaniform " and which occur in *Balaeniceps* but not in the storks and herons are as follows :

(1) Position of nasal groove along upper mandible, and strong terminal hook (see A(1) and A(2)).
(2) Arrangment of nasal cavity (see A(3) and A(4)).
(3) Relationship of bones of palate and maxillopalatines (see A(5)).
(4) Size of lachrymal and antorbital vacuity (see A(6)).
(5) Type of jaw articulation (see A(7)).
(6) Some features of the pectoral girdle and sternum (see B).
(7) Shape of first metacarpal (see D(3)).

In my opinion the skeleton of *Balaeniceps* has many points of similarity, due to convergence, with the Ciconiidae and Ardeae, but, in spite of its difference in outward appearance from any of the Pelecaniforms, it shares several apparently non-adaptive features with them. I find it difficult to account for this unless *Balaeniceps* is more closely related to the Pelecaniformes than it is usually considered to be. Therefore, from a consideration of the skeletal characters of *Balaeniceps rex*, it seems that this species could occupy a monotypic family in the order Pelecaniformes, possibly near the Pelecanidae.

SUMMARY

1. A number of features of the skeleton of *Balaeniceps rex* were found to be more like the pelicans than either the storks or herons, with which *Balaeniceps* is usually grouped.

2. A study of the literature showed that the pelican-like characters of *Balaeniceps* had never been fully investigated.

3. The skeleton of *Balaeniceps* was compared with those of all the families of the Pelecaniformes, except the Phaëthontidae, and with the Ardeidae, Cochlearidae and Ciconiidae of the Ciconiiformes. Reasons are given for limiting comparison to these groups.

4. The characters common to *Balaeniceps* and the Pelecaniformes are described in detail.

5. The osteological evidence suggests that *Balaeniceps* is more closely related to the Pelecaniformes than to the Ciconiiformes, and the family Balaenicipitidae may reasonably be placed in the Pelecaniformes, possibly near the Pelecanidae.

REFERENCES

BARTLETT, A. D. 1861. On the affinities of *Balaeniceps*. *Proc. Zool. Soc. London*, 1861 : 131–134.

BEDDARD, F. E. 1888. On certain points in the visceral anatomy of *Balaeniceps rex* bearing on its affinities. *Ibid.*, 1888 : 284–290.

BÖHM, M. 1930. Über den Bau des jugendlichen Schädels von *Balaeniceps rex* nebst Bemerkungen über dessen systematische Stellung und über das Gaumenskelett der Vögel. *Z. Morph. Ökol. Tiere, Berlin*, **17** : 677–718.

BONAPARTE, C. L. J. L. 1855. *Conspectus generum avium*, 1849–57. Lugduni Batavorum.

CAIN, A. J. 1954. Subdivisions of the genus *Ptilonopus*. *Bull. Brit. Mus.* (*nat. hist*) *Zool.* **2** (8) : 267–284.

DES MURS, M. O. 1859. Considérations oologiques sur l'oiseau type du genre Baléniceps. *Rev. et Mag. Zool.* Ser. 2, **11** : 477–481.

FÜRBRINGER, M., 1888 *Untersuchungen zur Morphologie und Systematik der Vögel.* **2** : 1187–1196. Amsterdam.

GADOW, H. 1893. Vögel : Aves in Bronn's *Klass. n. Ord. des. Thier-Reichs.* Bd. 6, Abth 4. Leipzig.

GIEBEL, C. G. 1873. *Balaeniceps rex. Z. ges. Naturw. Berlin*, **41** : 350–354.

GLENNY, F. H. 1955. Modifications of pattern in the aortic arch system of birds and their phylogenetic significance. *Proc. U.S. nat. Mus.* No. 3346, 104 : 525–621.

GOULD, J. 1852. On a new and most remarkable form in ornithology. *Proc. Zool. Soc. London*, 1851 (published 1852) : 1–2.

HEUGLIN, M. T. VON. 1856. *Systematische Uebersicht der Vögel Nord-Ost-Afrika's.* Wien.

—— 1873. *Ornithologie Nordost-Afrika's*, **3** : 1095–1099. Cassel.

JARDINE, W. 1852. Ornithology in 1850 ; *Balaeniceps rex. Contr. Orn.* 1851 (published 1852) : 11–14.

MAYR, E. & AMADON, D. 1951. A classification of recent birds. *Amer. Mus. Novit.* 1496.

MITCHELL, P. C. 1913. Observations on the anatomy of the Shoe-bill (*Balaeniceps rex*) and allied birds. *Proc. Zool. Soc. London*, 1913 : 644–703.

PARKER, W. K. 1860. Abstract of notes on the osteology of *Balaeniceps rex. Ibid.*, 1860 : 324–330.

—— 1861. On the osteology of *Balaeniceps rex. Trans. Zool. Soc. London*, **4** : 269–352.

—— 1862. [Letter on Reinhardt's 1861 paper.] *Ibis, London* : 297–299.

PYCRAFT, W. P. 1898. Contributions to the osteology of birds. I.—Steganopodes. *Proc. Zool. Soc. London*, 1898 : 83.

REINHARDT, J. 1860. On the affinities of *Balaeniceps. Ibid.*, 1860 : 377–380.

—— 1861. Some remarks on the genus *Balaeniceps. Ibis, London*, 1862 : 158–175. [Translation by A. Newton of article in *K. danske Vidensk. Selsk. Køben*h. 1861 : 135–154.]

SHUFELDT, R. W. 1901. Notes on the osteology of *Scopus umbretta* and *Balaeniceps rex. J. Anat. Physiol.* **2** : 405–412.

STRESEMANN, E. 1927–34. Aves in Kukenthal & Krumbach's *Handb. d. Zool.* Bd. 7 Hft. 2. Berlin and Leipzig.

TECHNAU, G. 1936. Die Nasendrüse der Vögel. *J. Orn. Leipzig.* **84** : 511–617.

VERHEYEN, R. 1953. Bijdrage tot de osteologie en de systematick der Anseriformes. *Gerfaut, Bruxelles*, 43. Supplement : 373–500.

WEINMANN, J. P. & SICHER, H. 1947. *Bone and Bones.* London.

WERNE, F. 1848. *Expedition zur Entdeckung der Quellen des Weissen Nil* (1840–41). Berlin.

WETMORE, A. 1930. A systematic classification for the birds of the world. *Proc. U.S. nat. Mus.* 76, **24** : 1–8.

—— 1951. A revised classification for the birds of the world. *Smithson. misc. Coll.* 117, **4** : 1–22.

PLATE

[Scale : The skulls have been variously reduced, so that the crania are of approximately the same size. The actual total length of each skull is given below in brackets.]
Lateral views of skulls of :

(1) *Balaeniceps rex* (265 mm.).
(2) *Pelecanus onocrotalus* (410 mm.).
(3) *Sula bassanus* (180 mm.).
(4) *Ciconia ciconia* (255 mm.).
(5) *Ardea goliath* (235 mm.).
(6) *Cochlearius cochlearius* (125 mm.).

E = external naris.
G = nasal groove.
H = premaxillary hook.
I =position of internal nares.
L =lachrymal.
M =maxillopalatine.
P =palatine.
V = antorbital vacuity.